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EFFECTS OF STRATOSPHERIC OZONE DEPLETION AND INCREASED LEVELS OF ULTRAVIOLET RADIATION ON SUBANTARCTIC FORESTS AND WESTERN PATAGONIAN STEPPE: A RESEARCH PROJECT

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Key words: forest, ozone depletion, PAR, photosynthesis, steppe, subantarctic, UV-B radiation

ABSTRACT

The depletion of stratospheric ozone is a well established fact, supported by remote sensing data. A corresponding increase of solar UV-B radiation reaching the surface of the Earth is being documented. The effects of this increment of UV radiation on living organisms are uncertain. Most of our knowledge of this problem is the result of laboratory experiments and studies on marine phytoplankton of Antarctica.

The purpose of this project is to identify and measure indicators of the effect of increased solar UV-B radiation on terrestrial plants. Our goal is to establish these indicators so that we may use them to predict the effects of further increased UV-B radiation on terrestrial ecosystems.

We propose a three year study of two parallel ecosystem types (forest and steppe) that run N-S over a 15° latitudinal gradient, along a gradient of ozone depletion over the mid-latitudes in Argentina.

Two stations to measure UV radiation and photosynthetically active radiation (PAR) will be installed along the gradient. We will use the same type of radiometer that is operated simultaneously with the spectroradiometer of the NSF Polar Program installed at Ushuaia, in Tierra del Fuego. The data of the latter will also be used in this project. Samples and *in situ* measurements will be taken at 10 sites on the gradient in the austral spring in each of the three years. The tasks we expect to perform at these 10 sites are 1) photosynthesis measurements, 2) chlorophyll concentration measurements, 3) leaf area and leaf area index (LAI) measurements, 4) epidermal pigments and soluble proteins extraction.

Intensive work will be performed at 3 sites (northern end, center, and southern end of the transect). The tasks described above will be performed, but we will also take a) productivity measurements, b) spectroradiometry, and c) collection of seedlings (and/or seeds) of *Nothofagus* spp., *Festuca gracillima*, *Poa* spp. *Rumex acetosa* and *R. acetosella*. A greenhouse experiment will be carried out in the southernmost site (Ushuaia). The seedlings (and seeds) collected at the three instrumented sites will be grown under ambient conditions and under UV filters. All the above measurements will be performed on these plants at regular intervals by the research team while in the study area and by local research staff for the remainder of the year.

We expect to produce and calibrate biochemical, botanical (LAI, and others), and spectroradiometric data. Our ground level measurements of UV radiation will be correlated to remote sensing data of ozone. The data will be used to generate response surface and other models of those variables controlled by UV radiation. In turn, these data will be used in ecosystem models in order to simulate the current conditions in both ecosystems and predict future developments under different scenarios. A point model will be developed which will then be applied at regional scale at selected locations along the gradient.

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This research will complement NASA's commitment to the study of stratospheric ozone. Southern Argentina is the most appropriate place for study as the largest UV effects on terrestrial ecosystems are expected there. Our findings may be relevant for human and all other forms of life. Furthermore, this research addresses several issues highlighted in the Working Document of April 4, 1993 on the U.S. Federal Government-Wide Ultraviolet-B (UV-B) Research Activity.

INTRODUCTION

"Little research has been done in this area, despite the potential for declines in agricultural yields as ozone concentrations continue to fall and UV-B radiation consequently continues to increase into the next century."

—NIE Network News, April 1993

The discovery of the Antarctic ozone hole in 1985 was a surprise to many researchers because it had not been predicted by any photochemical model and there was no immediately obvious explanation for it [50, 68]. However, the mechanism for this ozone loss was first postulated by Molina and Rowland in 1974 [41] who said that chlorofluorocarbons (CFCs) dissociate and liberate chlorine in the stratosphere where the chlorine catalyzes the breakdown of ozone. The consequent depletion of the ozone layer in the atmosphere causes an increase in incident solar ultraviolet (UV) radiation (280-400 nm) that impinges on the world's surface. (See Appendix for a summary of the biological effects of UV radiation). This mechanism has resulted in a large decrease in global ozone since about 1978 and a pronounced ozone hole in the southern hemisphere [27].

Natural and man-made causes coupled to produce a record low global ozone in 1992. Last year's ozone measurements were 2% to 3% lower than the lowest values recorded in earlier years. The lowest values of November and December 1992 were three to four standard deviations below the 12-year daily mean [21]. Although CFCs emissions have been sharply reduced in acceptance of the Montreal Protocol, a recent report [46] suggests that some CFCs may persist from three centuries to thousands of years. Further, harmful UV radiation may increase after volcanic eruptions [8,68] because volcanic plumes contain high concentrations of sulfuric acid droplets which can also reduce ozone column amounts either by enhancing chlorine-catalyzed chemistry or inducing convective lifting. The cause of the 1992 low ozone values is uncertain, but it is intuitively linked to the continuing presence of aerosol from the Mount Pinatubo eruption [21,35].

The 12% increase in harmful UV radiation resulting from a 9% decline in ozone at mid-latitudes [35] is currently linked to the augmented occurrence of biological phenomena such as skin erythema and cancer, cataracts, unusual pigmentation, and deformities and death of vascular plants. Since 1985, several phenomena directly attributable to this increased UV radiation have been found for phytoplankton [1,14,34,56], for terrestrial plants, and humans [37,17,29] in the Southern Hemisphere. A thinning ozone shield over the mid-latitudes and the Antarctic "ozone hole" are believed to be responsible for higher rates of human skin cancer in Australia, an apparently high incidence of cataracts in Patagonian sheep and Antarctic penguins, and lately, an increased red component in the canopies of the subantarctic forest of Patagonia (See Appendix, Part E).

Some side effects of increased UV with potentially large economic consequences include the possible collapse of complex aquatic food chains and lower crop yields which may force changes in the spatial location of agriculture. Studies conducted in Germany [18] have shown effects that impair the marketability of crops. These effects include overall size reduction, leaf size reduction, color changes, and morphology changes. (See Appendix C.)

Living systems have adapted to UV radiation mostly by filtering out the excess radiation with screening pigments [4,48]. (See Appendix, Part E). However, when these screening mechanisms fail, UV radiation causes different degrees of damage in plants, animals, and humans. In a recent statement in the

April, 1993 NIE Newletter the author said, "The only field data available on agricultural crops show a 20% decrease in yield in one soybean strain under increased UV-B radiation. In addition, laboratory studies appear to indicate that UV-B radiation alters the metabolism and growth of at least 50% of terrestrial plants." Investigated problems may have dramatic consequences on biotic productivity, survivability, and health of plants, animals, and man. Long-term ecological studies are needed to quantify the effects of increased UV radiation in the continents, assess the risks, and produce reliable data for prediction.

In response to increased UV radiation, the synergistic relationship among ecosystem components will produce effects that are nonlinear which will make it difficult to single out UV effects in field experiments [59]. Most of the regional data available on stratospheric ozone have been obtained by remote sensing studies of the thinning ozone layer so it is necessary to identify reliable terrestrial indicators of increased UV radiation. The thinned stratospheric ozone layer of the Southern hemisphere reaches as far north as approximately 34°S latitude [38,39,58]. Responses must be identified that can be easily measured and be unequivocally linked to increased UV radiation. If the production of screening pigments is an adaptive mechanism in plants, then a higher concentration of screening pigments in leaves may be interpreted as a natural response to increased UV radiation. If such higher concentrations of pigments filters out the excessive UV radiation, no damage will occur. If the screening effect is not sufficient then genetics, photosynthesis, growth, leaf shape and size, and pollen viability as well as pollen grain shape, size, and production may be affected by excessive UV radiation. It is necessary to monitor selected terrestrial ecosystems in sufficient detail to permit detection and interpretation of changes attributable to global climate change [13]. A model-guided design allows the prediction of systemic scenarios. At the same time, analytical models of ecosystem dynamics are necessary to determine the limits to which resilience of ecosystems can be stretched before they change, perhaps irreversibly [13].

OBJECTIVE AND HYPOTHESES

Objective: To quantify the responses of terrestrial vegetation to UV radiation by studying pigment concentrations, photosynthesis, and spectral parameters of selected plant species in the field and in greenhouses.

Hypothesis 1: Terrestrial plants respond to increased solar UV radiation by changing the concentration of pigments in leaves.

Hypothesis 2: UV-induced changes in the amount of plant pigment can be inferred from variations in spectral reflectances.

Hypothesis 3: If UV radiation increases beyond the filtering capacity of foliar pigments, changes will occur in foliar composition and fluxes of carbon.

PROPOSED RESEARCH

To evaluate the effects of increased UV-B radiation on land vegetation due to a thinning ozone shield, we propose a three-year study of forest and steppe of southern Argentina.

THE REGION

The deciduous formations of the subantarctic forests extend from 39°50'S to 55°S on the eastern slopes of the Andes (Figure 5). This narrow stripe enclosed by the 700 and 1,500 mm precipitation isopleths (Figure 1) is more dense from 41° to 46°S, then it occurs in patches down to 52°S and becomes dense again in Tierra del Fuego (54° to 55°S). This forest, which encompasses 15 degrees of latitude, is located on the continental landmass closest to Antarctica, and therefore is well suited as a field laboratory for the study of UV radiation effects on terrestrial plants. In contact with the forest, the western end of Patagonia is a narrow belt of open vegetation growing between the precipitation isopleths of 700 mm (forest limit) and 200 mm (Patagonia regime). Both formations extend under a gradient of 50% annual cloudiness in the north to 70% in the south (Figure 2). These features are relevant because the forest and the neighboring grass steppe run parallel to the gradient of ozone depletion in the southern Hemisphere reaching well into region affected by Antarctic ozone depletion, and the UV radiation on the Earth's surface may be either lower or higher with incomplete overcast [39] and this ecosystem extends under zones of 50, 60 and 70% cloud cover.

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Natural and man-made causes coupled to produce a record low global ozone in 1992. Last year's ozone measurements were 2% to 3% lower than the lowest values recorded in earlier years. The lowest values of November and December 1992 were three to four standard deviations below the 12-year daily mean [21]. Although CFCs emissions have been sharply reduced in acceptance of the Montreal Protocol, a recent report [46] suggests that some CFCs may persist from three centuries to thousands of years. Further, harmful UV radiation may increase after volcanic eruptions [8,68] because volcanic plumes contain high concentrations of sulfuric acid droplets which can also reduce ozone column amounts either by enhancing chlorine-catalyzed chemistry or inducing convective lifting. The cause of the 1992 low ozone values is uncertain, but it is intuitively linked to the continuing presence of aerosol from the Mount Pinatubo eruption [21,35].

The 12% increase in harmful UV radiation resulting from a 9% decline in ozone at mid-latitudes [35] is currently linked to the augmented occurrence of biological phenomena such as skin erythema and cancer, cataracts, unusual pigmentation, and deformities and death of vascular plants. Since 1985, several phenomena directly attributable to this increased UV radiation have been found for phytoplankton [1,14,34,56], for terrestrial plants, and humans [37,17,29] in the Southern Hemisphere. A thinning ozone shield over the mid-latitudes and the Antarctic "ozone hole" are believed to be responsible for higher rates of human skin cancer in Australia, an apparently high incidence of cataracts in Patagonian sheep and Antarctic penguins, and lately, an increased red component in the canopies of the subantarctic forest of Patagonia (See Appendix, Part E).

Some side effects of increased UV with potentially large economic consequences include the possible collapse of complex aquatic food chains and lower crop yields which may force changes in the spatial location of agriculture. Studies conducted in Germany [18] have shown effects that impair the marketability of crops. These effects include overall size reduction, leaf size reduction, color changes, and morphology changes. (See Appendix C.)

Living systems have adapted to UV radiation mostly by filtering out the excess radiation with screening pigments [4,48]. (See Appendix, Part E). However, when these screening mechanisms fail, UV radiation causes different degrees of damage in plants, animals, and humans. In a recent statement in the

April, 1993 NIE Newletter the author said, "The only field data available on agricultural crops show a 20% decrease in yield in one soybean strain under increased UV-B radiation. In addition, laboratory studies appear to indicate that UV-B radiation alters the metabolism and growth of at least 50% of terrestrial plants." Investigated problems may have dramatic consequences on biotic productivity, survivability, and health of plants, animals, and man. Long-term ecological studies are needed to quantify the effects of increased UV radiation in the continents, assess the risks, and produce reliable data for prediction.

In response to increased UV radiation, the synergistic relationship among ecosystem components will produce effects that are nonlinear which will make it difficult to single out UV effects in field experiments [59]. Most of the regional data available on stratospheric ozone have been obtained by remote sensing studies of the thinning ozone layer so it is necessary to identify reliable terrestrial indicators of increased UV radiation. The thinned stratospheric ozone layer of the Southern hemisphere reaches as far north as approximately 34°S latitude [38,39,58]. Responses must be identified that can be easily measured and be unequivocally linked to increased UV radiation. If the production of screening pigments is an adaptive mechanism in plants, then a higher concentration of screening pigments in leaves may be interpreted as a natural response to increased UV radiation. If such higher concentrations of pigments filters out the excessive UV radiation, no damage will occur. If the screening effect is not sufficient then genetics, photosynthesis, growth, leaf shape and size, and pollen viability as well as pollen grain shape, size, and production may be affected by excessive UV radiation. It is necessary to monitor selected terrestrial ecosystems in sufficient detail to permit detection and interpretation of changes attributable to global climate change [13]. A model-guided design allows the prediction of systemic scenarios. At the same time, analytical models of ecosystem dynamics are necessary to determine the limits to which resilience of ecosystems can be stretched before they change, perhaps irreversibly [13].

OBJECTIVE AND HYPOTHESES

Objective: To quantify the responses of terrestrial vegetation to UV radiation by studying pigment concentrations, photosynthesis, and spectral parameters of selected plant species in the field and in greenhouses.

Hypothesis 1: Terrestrial plants respond to increased solar UV radiation by changing the concentration of pigments in leaves.

Hypothesis 2: UV-induced changes in the amount of plant pigment can be inferred from variations in spectral reflectances.

Hypothesis 3: If UV radiation increases beyond the filtering capacity of foliar pigments, changes will occur in foliar composition and fluxes of carbon.

PROPOSED RESEARCH

To evaluate the effects of increased UV-B radiation on land vegetation due to a thinning ozone shield, we propose a three-year study of forest and steppe of southern Argentina.

THE REGION

The deciduous formations of the subantarctic forests extend from 39°50'S to 55°S on the eastern slopes of the Andes (Figure 5). This narrow stripe enclosed by the 700 and 1,500 mm precipitation isopleths (Figure 1) is more dense from 41° to 46°S, then it occurs in patches down to 52°S and becomes dense again in Tierra del Fuego (54° to 55°S). This forest, which encompasses 15 degrees of latitude, is located on the continental landmass closest to Antarctica, and therefore is well suited as a field laboratory for the study of UV radiation effects on terrestrial plants. In contact with the forest, the western end of Patagonia is a narrow belt of open vegetation growing between the precipitation isopleths of 700 mm (forest limit) and 200 mm (Patagonia regime). Both formations extend under a gradient of 50% annual cloudiness in the north to 70% in the south (Figure 2). These features are relevant because the forest and the neighboring grass steppe run parallel to the gradient of ozone depletion in the southern Hemisphere reaching well into region affected by Antarctic ozone depletion, and the UV radiation on the Earth's surface may be either lower or higher with incomplete overcast [39] and this ecosystem extends under zones of 50, 60 and 70% cloud cover.

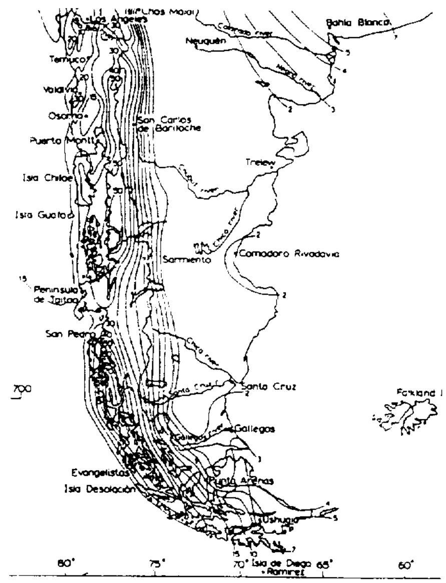

Fig. 1. Annual precipitation in dm. (from Prohaska [45], modified).

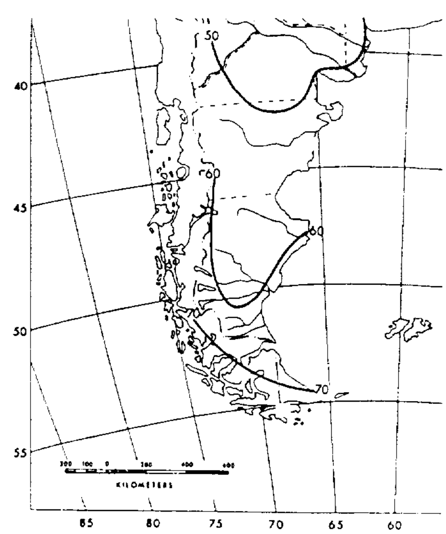

Fig. 2. Annual cloudiness in percent of sky cover (from Prohaska [45], modified).

UV RECORDING STATIONS

Two stations (equipped with five-channel radiometers designed to monitor UV irradiance by sensing four critical spectral regions in the UV-B and UV-A ranges), will produce a continuous record of UV radiation received at the surface. One station is already in Ushuaia (the site of one of NSF's UV-monitoring stations). At the other two stations, Bariloche and Lago Viedma, we will establish ground-based UV radiometers manufactured by Biospherical Instruments. These instruments measure and record UV-A, UV-B, and PAR (Photosynthetically Active Radiation). University personnel will check the instruments daily to ensure that all equipment is operating properly. Failures will be reported to the University of Mar del Plata for prompt servicing.

GREENHOUSE EXPERIMENT

As is known from the classic studies of Clausen et al. [12] and Hiesey et al. [28], plants of the same species collected across a transect can show marked ecotypic and phenotypic variation. To account for these differences, seedlings from selected points along the latitudinal gradient will be brought to Ushuaia. *Nothofagus antarctica* (Forster f.) Oersted, *N. pumilio* (Poeppig and Endl.) Krasser, the evergreen species, *N. betuloides* (Mirbel) Oersted, and steppe species including *Festuca gracillima* Hooker f., *Poa* spp., *Rumex acetosa* L., and *R. acetosella* L. will be grown in a greenhouse under total UV screening (control) and natural conditions (treatment). A robust experimental design (latin square and the like) will be used to allow application of statistical techniques for the analysis of data on growth and pigmentation. This experiment will play a major role in the testing process of Hypothesis 1. Non-destructive hemispherical reflectance measurements will be obtained with a spectroradiometer during the control period. Large numbers of seedlings will be grown in each experiment in order to provide sufficient materials for the necessarily-destructive techniques of pigment analysis. A sub-sample of the leaves will be removed for chemical analysis of pigments. This experiment will be performed in real time in connection with the NSF Polar Program* recording stations in order to obtain a simultaneous record of biological variables and UV radiation. The measurements will include UV and PAR modules as parts of complete and automatic weather stations.

HYPOTHESIS TESTING

We will test our hypotheses using forest and grassland species that span the latitudinal belt. Two deciduous arboreal species, *Nothofagus antarctica* and *N. pumilio*, found from 36°S to Tierra del Fuego, and an evergreen species, *N. betuloides* (46°40'S to Tierra del Fuego) will be studied to evaluate the responses of forest vegetation to increased solar UV radiation. *Festuca gracillima*, *Poa* spp., *Rumex acetosa* L., and *R. acetosella* L. will also be studied in this project. In the south, the Magellan sector of Patagonia (51-54°S) is a steppe that grows on the soils developed on the moraines of the last Ice Age.

TEST OF HYPOTHESIS 1

Biochemistry. To verify if the ozone depletion gradient generates parallel responses in plants, pigment analysis of leaves of *Nothofagus* spp. growing on the east Andean slope will be performed at 10 sites from 36° to 55°S. The neighboring steppe will serve to test the effects of increased UV radiation on open vegetation. Plants to be tested are autoctonous grasses (*Festuca* spp. and *Poa* spp.), and introduced weeds, *Rumex* spp. [41]. Extractions will be performed in the field with 70-80% methanol (with the addition of 0.1% hydrochloric acid to preserve anthocyanins). A study of the crude extract will be performed by two-dimensional paper or thin-layer chromatography [22]. Qualitative and quantitative analyses will be performed with a combination of paper chromatography, UV spectroscopy, and, specially, by high performance liquid chromatography (HPLC) in reversed-phase columns (C18), eluted in a gradient of methanol or acetonitrile [25]. Flavonoids will be detected by fluorescence or by absorbance at 355 nm. Additionally, the content of soluble proteins in leaves will be

* The National Science Foundation's (NSF) Polar Program has established a UV monitoring network in the western hemisphere. There are presently five stations in operation: Three in Antarctica, one in Ushuaia, Argentina, and one in Barrow, Alaska. The ground stations utilize spectroradiometers built by Biospherical Instruments, Inc. (San Diego, California). Data scans are conducted on an hourly basis when the sun is above the horizon are distributed, after calibration, on CD-ROM. These stations were established to provide independent confirmation of the role of the ozone layer in moderating UV irradiance [6].

analyzed. Leaf tissue will be homogenized and extraction with trichlorhydric buffer, 50 mmolar at pH 8.0 will be done. Quantification will be based on the measurement of peptide bonds. Results will be related to dry weight and other parameters.

TEST OF HYPOTHESIS 2

Leaf-level measurements. The green leaf reflectance curve in the visible region of the electromagnetic spectrum is characterized by absorption of incident radiation by plant pigments, particularly chlorophyll. Leaf spectra from various plant species have been used to estimate leaf nitrogen content [65,66], chlorophyll concentrations [66], and leaf water content [64]. Light absorption by water in intracellular spaces of leaves dominates reflectance in the short wave infrared region. A shift in plant pigment production, from chlorophyll to accessory pigments, can result in a corresponding spectral response in the visible region of the spectrum.

We will use individual leaf spectrometry for assessing the early response of *Nothofagus* spp. to UV-induced stress. A Spectron SE-590 spectroradiometer with an integrating sphere attachment will be used in the field and in the greenhouse (under two treatments: ambient and UV-restricted) to acquire hemispherical reflectance data from individual leaves. The leaves subsequently will be analyzed for chlorophyll, anthocyanins, flavonoids, carotenoids, and other pigments and secondary metabolites. Statistical analysis will determine the relationship of spectral data to variations in foliar pigment concentrations. [We are aware that there are procedural problems with the calibration of different SE-590 instruments (S. Goward, personal comm.).] Our use of the SE-590 will ensure that spectral measurements will be consistent within the proposed study.)

Leaf Area Index. Variations in plant biophysical parameters such as leaf area index (LAI) have been used for spectrally separating healthy from stressed plant canopies [36]. The LAI has been correlated with near-infrared to red wavelength ratios [15,43,57]. The LAI of *Nothofagus* forests will be estimated in the field using a Decagon ceptometer [44]. These measurements will be related to spectral ratios obtained from remote sensing data used in other research work. Remotely sensed estimates of LAI will be used in the ecosystem simulation models (see below).

TEST OF HYPOTHESIS 3

Modeling. Ecosystem modeling is a method to integrate and balance the opposing or compounding effects of increased solar UV radiation on plant molecular, cellular, and production processes. Our modeling will be carried out in two interdependent phases: (1) development of a point model and (2) application of the model on a regional scale, extending along the UV radiation gradient.

Forest vegetation model. Greenhouse measurements taken for the six species will provided data to test Hypothesis 3 and data to establish parameters of physiologically detailed models of forest and grassland ecosystems. The models can extrapolate greenhouse results to predict whole plant and ecosystem level responses to UV-B chronic exposure. Experimental measurements include leaf physical characteristics, composition, pigmentation, flux rates, and environmental conditions needed for testing Hypothesis 3.

Leaf physical characteristics are measured to quantify if either leaf area or specific leaf area changes with UV-B exposure as has been reported by Tevini [60,61]. The data also are needed to scale up flux measurements to plant levels because ecosystem models use a leaf biomass-to-area relationship in scaling up modeled leaf processes [50].

Leaf composition includes nitrogen and lignin concentrations which should correspond to enzymatic activity and leaf construction costs [52]. Leaf nitrogen is a critical parameter for both photosynthesis and respiration modeling [51,52]. Increased nitrogen usually causes an increase in both modeled respiration and photosynthesis rates. UV-B damaged leaves can have high leaf nitrogen concentrations but low photosynthesis rates [61]. Biochemical parameters in detailed photosynthesis models [19] can be altered to reflect changes in photosynthesis rates per leaf nitrogen concentrations. For estimating growth respiration and for long-term plant and ecosystem modeling, changes in leaf lignin are important because lignin has higher construction costs than carbohydrates (2.2 vs. 1.2 g/g) [53] and as litter, lignin slows decay which in turn slows soil nitrogen cycling rates and lowers soil nitrogen availability.

Carbon fluxes will be measured both at optimum photon flux densities and at night for each of the six species using the LICOR photosynthesis meter. The maximum photosynthesis and night respiration estimates will be made before the destructive leaf pigmentation testing in Hypothesis 1 and 2. Photosynthesis rates will be related to leaf composition and leaf structure for whole plant totals. Appropriate photosynthesis model adjustments reflect UV-B damage that can be made to mechanistic rubisco-nitrogen relationships or made by lowering maximum photosynthesis rates. Plant maintenance respiration, defined as a model parameter (g/c per g/living tissue), will be measured for leaves and estimated for stem and root tissues keeping in mind that respiration is temperature sensitive (Q10) and respiration coefficients are a function of total nitrogen [52] and UV-B exposure.

Ecosystem model extrapolations will integrate the leaf and tissue changes to show long-term changes in LAI, NPP, and litter decomposition. For the forest ecosystems, modifications will be made to the Forest-BGC ecosystem model [50,51] including sections of Biome-BGC [31] to replace the less detailed leaf physiology as needed by this experiment.

Steppe Vegetation Model. This model will be used in the Magellan steppe to simulate hydrology, snow accumulation and melt, plant growth, and mortality. Ecological differentiation between the simulated species will be accomplished by using different parameters for the different plant species simulated by the model. Thus grasses, forbs, and shrubs in the Patagonian steppe can be simulated by using a standard set of parameters modified to distinguish between the functional groups or plant species. Specific biomass levels required for input to the model will be measured during the field data-gathering efforts.

By studying grasses, critical differences between growth cycles of species groups that occur during the UV increase episodes can be seen. The ozone hole opens over the Antarctic in August and closes in November. This is the time some grasses, including *Festuca* spp., *Poa annua,* and *P. trivialis*, (the early flowering group or EFG) initiate flowering. At about the time the hole closes, other species (*Festuca purpurascens, Lolium multiflorum, Poa scuberula*, the late flowering group, LFG) initiate the flowering cycle. This might mean that the overt/direct effects of UV will be exerted primarily on the EFG of the grassland communities. These effects can be simulated by modifying the parameters that control the production of photosynthate [4,10] for the EFG while keeping the LFG parameters unchanged. Measurement of rates of photosynthesis for steppe vegetation is therefore important, since this will indicate carbon flux of above-ground plant components and thus give an estimate of steppe production. To test these ideas, direct and continuous recording of the UV radiation reaching the surface at the site of the experiments is needed.

Further, it has been postulated that the growth rates of plant parts will also change in response to higher UV as will some competitive interactions [10]. The model to be used will need a plant component with explicit relationships for allocation and competition. It will be used to simulate these changes in the steppe vegetation of the study area. The changes in the state variables will then give an indication as to how the grassland ecosystem will change.

We can postulate at this point that plant community composition might change because of the different amounts of time the EFG and LFG components of the grassland are exposed to UV. Because different plants have different optimal photosynthetic rates, we can expect that these rates (for the EFG) will change with UV exposure [10], changing the water uptake and transpiration rates of these plants. This will affect the water balance for the site and favor one group over the other to a greater extent than at present, thereby altering the species composition of the community. Although conducted under simulated severe ozone depletion (40%), the experiments of competing pairs of weeds and crops that were cited by Tevini [62] well illustrate our ideas regarding the Magellan steppe.

CREATION OF DATABASES

TOMS Data. The Total Ozone Mapping Spectrometer (TOMS) has acquired daily global ozone data from October 1978 to May 1993. An historical database is available from NASA's Climate Data System (NCDS) and from CD-ROM. Figure 3 shows total column ozone data computed using a 100-day moving average for Ushuaia, Argentina [6]. This figure depicts a decreasing trend in ozone between 1979 and 1991, suggesting a possible parallel trend in the short-wavelength UV radiation incident on the Earth at this location. The amount of UV radiation reaching the Earth's surface is not only dependent on the amount of stratospheric ozone but is also a

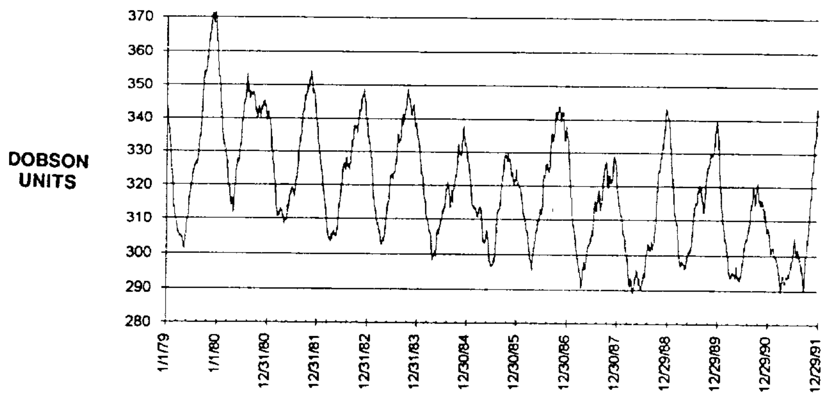

Fig.3. Total column ozone over Ushuaia (1978-1991) computed with a 100-day moving average (from Booth et al. 1992 [6], modified).

function of solar angle and cloud cover. This is particularly relevant for the longer wavelengths of UV-A. For the shorter wavelengths of UV, however, dramatic differences in UV irradiance have been correlated with ozone depletion [6].

Other Databases. Large amounts of data will be produced by this research work. We will file those data in ASCII and in common database programs to make the dataset available to future users. Data to be filed are: UV and PAR, climate, photosynthesis, respiration, chlorophyll concentration, leaf area, leaf area index, leaf weight, total leaf nitrogen, pigments, soluble proteins, productivity (including pollen), radiometry, and spectroradiometry.

EXPERIMENTAL PLAN AND TIME TABLE

We will establish a transect in Argentina that runs north to south for approximately 1,500 km. The transect will have three stations (Table 1) in an area where we have been promised the use of facilities. The southernmost station on the transect will be at Ushuaia in Tierra del Fuego and will be our base station and the site of our greenhouse experiments.

Field work must start in beginning of October and extend into November. The Antarctic "ozone hole" begins to form in August and is largest in early October then dissipates in November. It is springtime there, soil moisture has been replenished by winter precipitation, and the trees are ready to produce flowers and new leaves.

If we assign two days per sampling site and two days to setup the group of collaborators and equipment in Mar del Plata plus a minimum loss due to unfavorable weather conditions, three weeks will be devoted to sampling along the transect. The remaining time will be used to work in the greenhouse experiment in Ushuaia. In addition, a greenhouse facility will be established in Tierra del Fuego which O.A. Bianciotto will supervise after the field season and take the responsibility for recruiting students of National University of Patagonia. These students will be responsible for the control and maintenance tasks of the greenhouse experiments.

FIELD WORK

We will proceed from the north to the south along the margin of the forest, starting at Bariloche and traveling the distance to the southern end of the transect, sampling at regular intervals, one team in the forest and one team in the steppe or grassland areas. This will require two vehicles, one of which will be provided by the University of Mar del Plata. As shown in Figure 4, ten prospective sites have been selected for this study. Each site will be marked by a portable global positioning system (GPS) to enable us to retrace it in each of the subsequent years of the study. At each location, both the forest team and the steppe team will perform:

- photosynthesis measurements (LICOR photosynthesis meter)
- chlorophyll concentration measurements using a SPAD 502 instrument
- leaf area measurements
- pigments and soluble proteins extraction

Intensive work will be performed in three of these sites (~40°; ~50° and ~55°S) where precise and continued UV radiation and weather measurements will be taken. This work will be in addition to the standard measurements (listed above), and include

- meteorological measurements
- productivity measurements
- spectroradiometer measurements
- seeds and/or seedlings of *Nothofagus antarctica*, *N. pumilio* and *N. betuloides* (in Bariloche and Ushuaia) as well as *Festuca gracillima* (native), and *Rumex acetosa*, *Rumex acetosella*, *Poa annua* and *P. pratensis* (alien) will be collected and trans ported for growth in the greenhouse at Tierra del Fuego.
- Further analyses of all studied materials include weight, total leaf nitrogen, lignin.

SCHEDULE

July 1993-June 1994:

1) Cooperative agreements between NASA and Argentine institutions (Government, universities, hospitals, schools, private citizens)
2) Cross-calibration of UV radiometers with NSF unit at Ushuaia.
3) Installation of UV recording stations. Initial database construction
4) Pigment and soluble protein analyses.
5) Preparation and initiation of greenhouse experiments in Tierra del Fuego
6) Spectral measurements—leaf level (mature trees)
7) Cross-calibration of UV radiometers with NSF unit at Ushuaia
8) Analysis of TOMS data

July 1994-June 1995:

1) Repetitions of 1993 experiments (adjusted in the light of the acquired experience)
2) Spectral measurements—leaf level (seedlings)

Table I. Proposed UV Study Sites.

Site No.	Location	Latitude	Longitude	Elevation (m)
1	S.C. de Bariloche	41° 06' S	71° 10' W	836
2	Lago Viedma	49° 30' S	72° 30' W	350
3	Ushuaia	54° 48' S	68° 19' W	6

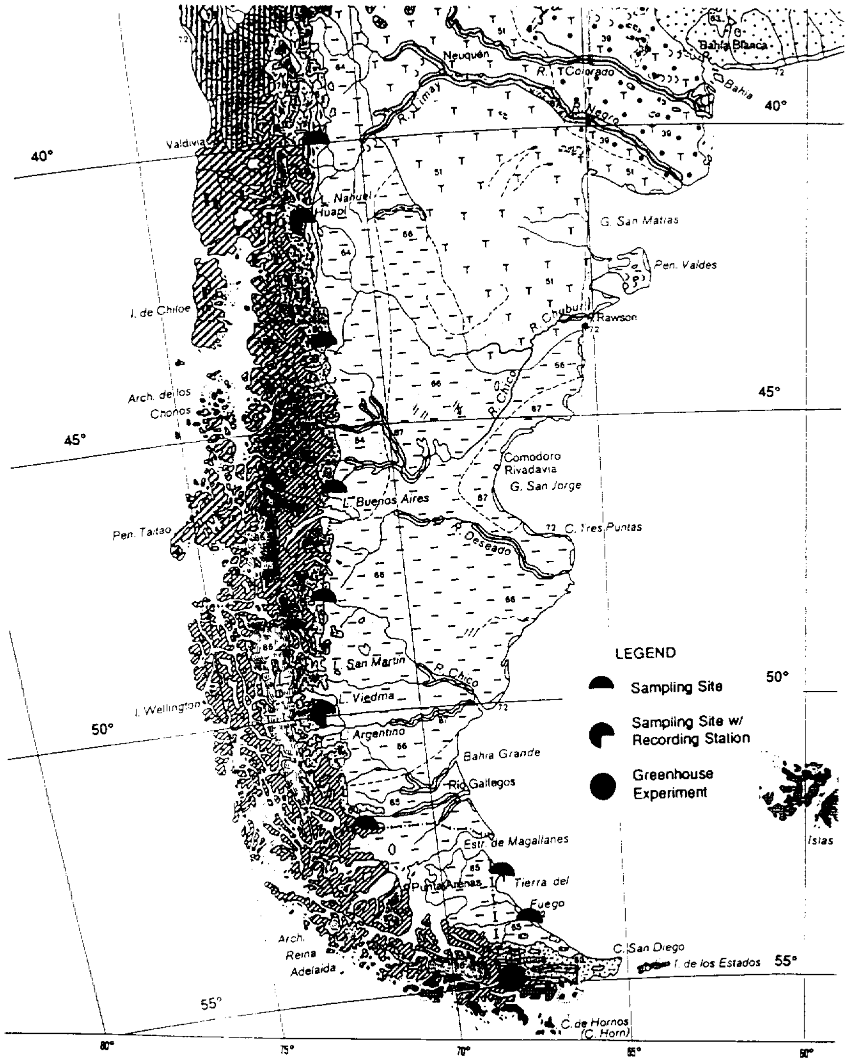

Fig.4. The ten sites selected for this study. The extent of studies to be undertaken at each site is indicated by the legend. (From Hueck & Seibert 1981 [30], modified).

July 1995–June 1996:

1) Repetitions of 1993, 1994 experiments
2) Use of steppe vegetation models on Magellan steppe
3) Use of forest vegetation models on Subantarctic forest

EDUCATION OUTREACH

Students of American, Argentine, and German universities will be admitted for technical work in the project that may eventually be used for M.S. theses or Ph.D. dissertations.

ANCILLARY AND FUTURE RESEARCH

1) *Pollen studies*. It has been suggested that pollen viability is impaired by increased UV-B radiation [20]. South American *Nothofagus* expose their pollen-producing primordia as the Antarctic ozone hole opens and enter into anthesis during the maximum ozone hole and persist until the hole closes. The entire Subantartic Forest Ecosystem is located under the ozone depleted zone (since 1983 in the range of 350 Dobson units). Increased solar UV-B radiation resulting from such ozone depletion may be affecting not only the viability of the pollen but also its ontogenic process and hence its production, morphology, and size distribution. This general assumption has an impact on several areas of research and a number of hypotheses can be formulated and tested.

2) *Leaf morphology and anatomy studies*. Some cell structural components absorb in the UV-B range. Plants may respond to increased solar UV-B radiation by increasing the proportion of those components. Classical anatomic studies of leaves of both evergreen and deciduous species of *Nothofagus* and on leaves of *Rumex* spp. from 10 sampling sites may help understand other UV effects on plants.

3) *Plant embryology studies*. Plants may be affected by increased UV radiation in early stages of development because IAA is a UV target. We will invite Alfredo Cocucci (University of Cordoba) to initiate a research work on embryons of *Nothofagus* spp. and *Rumex* spp.

4) *DNA alteration studies*. A major target of UV radiation, DNA from samples taken at all 10 sites and the Ushuaia Greenhouse Experiment will be studied at the ARC by a post-doctoral fellow (Charles Cockell), under the guidance of Lynn Rothschild. Experiments in growth chambers will be conducted at the ARC under controlled (realistic) conditions.

5) *Public health*. During the field work season we expect scientific interaction with physicians in Patagonia and Tierra del Fuego. We will encourage them to keep a record of patients treated for erythema, skin cancer, and vision ailments (cataracts and the like). We will encourage joint research efforts taking advantage of our direct UV-B measurements and our capability to perform statistical analysis. We have already taken some steps in this direction.

Acknowledgments

We would like to acknowledge with thanks J.Brass, E.Condon, P.Matson, L.Morrissey, D.Peterson, P.Russell, J.Sharp and O.Toon (NASA/Ames Research Center) who reviewed an earlier version of this article and made valuable suggestions. The comments by R. Hilton Biggs (University of Florida) are also greatly appreciated.

APPENDIX

BIOLOGICAL EFFECTS OF UV RADIATION

The damaging effects of UV radiation occur at two major levels of organization:

Molecular Level. UV radiation affects nucleic acids, membranes, and phytohormones. Due to the aromatic-electron system, purine and pyrimidine bases of nucleic acids have a strong absorption near 260 nm. The aromatic amino acids included in protein molecules bring protein maximum absorption down to 280 nm. Abscisic acid (AA) and indole acetic acid (IAA) also absorb in the UV range (Figure A1). The action spectrum for killing bacteria peaks near 265 nm which is close to the absorption spectrum of DNA, suggesting that DNA is the target. However, wavelengths shorter than 280 nm do not reach the Earth's surface.

Cellular Systems. The mutagenic power of UV radiation is exercised on DNA molecules of viruses, prokaryotic, and simple eukaryotic organisms. Experiments on advanced eukaryotic cells have shown a still higher sensitivity to UV radiation [23]. The possible targets are DNA and proteins. The uncovered epidermis of many vertebrates is the main target for UV radiation. Short-term radiation can induce tanning and synthesis of vitamin D. Longer exposures result in erythema (sunburn) and can induce degenerative skin diseases and tumors [23].

EFFECTS OF INCREASED UV RADIATION ON TERRESTRIAL PLANTS

The effects of increased UV radiation on terrestrial life forms are probably best recorded by plants. In fact, increased UV radiation affects:

A. *Photosynthesis*. Increases of UV-B radiation (280-320 nm) equivalent to atmospheric ozone reductions of 50% or less adversely affect various component reactions of photosynthesis and carbon assimilation rates. UV-B has been linked to disruptions of the chloroplast envelope in *Beta vulgaris* [2,7,55], *Glycine max*, and *Rumex patientia* [11]. In all these studies, damage appeared to accumulate with duration of dose (Sisson 1986). The action of moderate levels of UV-B radiation on photosynthesis seems to concentrate on photosystem II (PS II), while photosystem I (PS I) remains unaffected. The impairment of PS II activity by UV-B radiation is due to blockage of PS II reaction centers rather than an inhibition of the water-splitting enzyme system [32,42]. Under a regional or even global perspective, the initial question to be addressed is whether chlorophyll concentrations are altered in plants exposed to UV-B radiation levels equivalent to a reduction in atmospheric ozone of less than 20% under field conditions [54]. Plants with photosynthetic C3 pathways are significantly affected by increased UV-B radiation while those with C4 pathway remain relatively unaffected [3]. Several authors [18,62,69] have found increased concentrations of soluble proteins in leaves of plants exposed to several levels of UV-B radiation [57].

B. *Carbon assimilation*. The detrimental effects of UV-B radiation on carbon assimilation have been extensively documented. Although physiologically sound, much of the available information on carbon assimilation has been obtained under conditions that were too artificial to be considered valid (i.e., under low visible light flux that is known to enhance the deleterious effects of UV-B radiation). It is therefore necessary to carry out studies under ambient conditions equivalent to a reduction of 20% or less of atmospheric ozone. A central question in carbon assimilation is whether the repression of photosynthesis is dose-dependent and cumulative and, hence, if reciprocity is maintained. The latter was demonstrated in several experiments [47,54]. Reduction of photosynthesis was evident during the early stages of leaf ontogeny.

C. *Growth*. Indole acetic acid (IAA) in plant meristems is a target of UV-B radiation [4,63]. Tevini and Iwanzik [63] observed that growth is slower as increased UV-B is experimentally applied to *Cucumis sativus* plants. They conclude that moderate enhancements of UV-B radiation (such as that resulting from small stratospheric ozone depletions) will cause significant reductions in growth of sensitive cucumber seedling. *Hordeum* sp. seedlings irradiated with UV-B have disturbed vertical growth, suggesting destruction of IAA molecules in the leaf tips. Leaf structure [7], nucleic acids, and pollen [20] are also affected. The experiment described by Tevini [61] reinforces these views. The conditions of such experiments (25% increase of solar UV-B radiation equivalent to a 12% ozone depletion) are similar to the ones prevalent at the latitude of Ushuaia [38,39]. This fact gives additional meaning to our LAI measurements along the gradient of ozone depletion.

D. *Plant Pathology*. Biggs and Webb [5] investigated yield and disease incidence and severity for wheat (*Triticum aestivum*) in connection with enhanced UV-B radiation in field conditions. They concluded that susceptibility to leaf rust (*Puccinia recondita* f. sp. *tritici*) is increased by enhanced UV-B radiation.

E. *Protective Mechanisms*. As stated by Beggs et al. [4], protective mechanisms can be grouped in three main classes: (1) UV damage reparation or effects negation, (2) reduction of the amount of UV radiation actually reaching sensitive targets, and (3) responses that minimize the negative effects or damages. These mechanisms may always be present or appear as the plants develop normally, without any special outside stimulus [4]. Structural attenuation plays little role in most plants [10]. Cuticles and cell walls do not absorb UV radiation. Sometimes cuticles (often thickened cuticles) are covered by external secretions of powders with flavonoids as well as waxes, oils, and some alcohols, all of which absorb UV radiation efficiently (4,16,33,72]). The mechanisms of reduction of the amount of UV radiation reaching sensitive targets are relevant for this project.

SCREENING PIGMENTS

It has been suggested [4,9,71] that, as one of their mayor functions, anthocyanins and flavonoids absorb UV radiation that might otherwise cause damage to the plant. These views are based on the fact that flavonoid synthesis is often stimulated by radiation, via phytochrome and/or the blue light receptor or induced by UV-B radiation [71]. As anthocyanins are not efficient UV screens, they need to be either esterified with cinnamic acids or to be present in very high concentrations [61]. This fact leads us to believe that some changes may be observed in the spectral signature of vegetation under UV stress. There are three further reasons to consider this as a protective mechanism: (1) the highest quantum efficiency occurs at the most damaging wavelengths reaching the Earth's surface (about 300 nm), (2) there is a linear fluence-effect relationship, and (3) the response after UV induction is quick [70,71]. Anthocyanins and flavonoids are located in epidermal cell vacuoles, although flavonoids also occur in chloroplasts. UV-B radiation stimulates the synthesis of epidermal pigments (flavone glycosides and anthocyanins) that absorb in the UV range and protect inner foliar tissues, but UV-induced reduction of photosynthesis shows that some UV reaches the inner tissues of the leaf [23]. Experiments in high latitudes have shown that increased UV-B irradiance inhibits photosynthesis and increases accumulation of UV-absorbing pigments in the leaves [26]. UV-induced decrease in mitosis frequency in *Rumex* spp. shows that UV damages the DNA molecule. It has been shown that the synthesis of flavonoids is activated by stress, including UV irradiation [24]. This indicates the existence of UV-activated promoters. Although the enzymes for flavonoid synthesis are involved in other pathways, conducting to phytoalexins and lignin, the increase in intermediates of pigment biosynthesis can explain the detected accumulation of UV-absorbing pigments in leaves [26]. Some flavonoids and anthocyanins also absorb in the visible. Therefore, it might be possible to identify changes in spectral signatures of vegetation exposed to enhanced UV-B radiation.

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